Biological Control 67 (2013) 328–336

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Behavior of *Montandoniola confusa* Streito & Matocq (Hemiptera: Anthocoridae) preying upon gall-forming thrips *Gynaikothrips ficorum* Marchal (Thysanoptera: Phlaeothripidae)

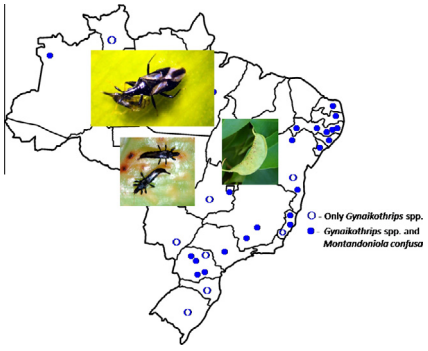
Adauto M. Tavares [a], Jorge B. Torres [b,*], Christian S.A. Silva-Torres [b], Alessandra M. Vacari [c]

[a] Embrapa Amazônia Ocidental, Rodovia AM-010Km 29, Zona Rural – CEP 69010-970, Caixa postal 319 Manaus, Amazonas, Brazil
[b] Departamento de Agronomia, Entomologia, Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros s/nDois Irmãos, 52171-900 Recife, Pernambuco, Brazil
[c] Departamento de Fitossanidade, Faculdade de Ciências Agrárias e Veterinárias FCAV/UNESP, 14884-900, Via de Acesso Prof. Paulo Donato Castellane s/n, Jaboticabal, São Paulo, Brazil

HIGHLIGHTS

- The thrips *Gynaikothrips ficorum* and its predator *Montandoniola confusa* are associated and spreading alongside one another throughout Brazil.
- *M. confusa* prey upon all thrips life stages and exhibits a type II functional response.
- It is estimated ~10-fold greater predation on eggs compared to larvae/prepupae and adult thrips.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 28 May 2013
Accepted 5 September 2013
Available online 17 September 2013

Keywords:
Predation
Functional response
Prey defense
Prey preference

ABSTRACT

The gall-forming thrips *Gynaikothrips ficorum* Marchal (Thysanoptera: Phlaeothripidae) is recorded in all regions where its host plant, *Ficus microcarpa* (Marchal) (Moraceae), has been cultivated as an urban and interior landscape plant species, including potted plants and bonsai. Similarly, the thrips predator *Montandoniola confusa* Streito & Matocq (Hemiptera: Anthocoridae) has generally followed the prey distribution. The gall induced by thrips degrades the plant foliage, and the thrips themselves can be annoying for people both outdoors and indoors. The galls, however, create a microcosm with all developmental stages of the thrips and its predator. In this study we present the first records of *M. confusa* in South America, document the species' widespread concomitant occurrence across Brazil, and report our studies of three aspects of *M. confusa* predation upon the eggs, larvae/prepupae, and adults of *G. ficorum* thrips: (i) functional response of the predator adult female as a function of different densities of thrips eggs, larvae/prepupae and adults separately: (ii) predation on eggs by adult *M. confusa* with adult thrips present in the gall; and (iii) adult *M. confusa* prey preferences when all thrips stages occurred simultaneously in the gall. For all three thrips life stages tested, the predator exhibited a type II functional response. Despite the availability of different life stages in the gall, *M. confusa* adults are capable of preying upon all life stages of *G. ficorum*, predation was preferentially on thrips eggs, with an estimated ~10-fold greater predation on eggs compared to larvae/prepupae and adult thrips. Egg predation was unaffected by the presence of defensive adult thrips in the gall under low densities (<30 eggs/gall) but when egg densities were greater than 30 eggs/gall, it was reduced when adult thrips were present. However, the relative number of thrips adults per gall did not statistically change the outcome.

* Corresponding author. Fax: +55 81 3320 6205.
E-mail address: jtorres@depa.ufrpe.br (J.B. Torres).

1049-9644/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.biocontrol.2013.09.004

1. Introduction

Species of *Montandoniola* are predators of gall-forming thrips, including 20 species of Phlaeothripidae and five species belonging to the genus *Gynaikothrips* (Dobbs and Boyd, 2006; Yamada et al., 2011). According to Pluot-Sigwalt et al. (2009), the predator *Montandoniola confusa* Streito & Matocq has been erroneously cited as *Montandoniola moraguesi* (Puton) or *Macrotrachiella nigra* Parshley in the Americas. Therefore, data published in the Americas referring to those two species should be applied to *M. confusa*. Further, based on the data reviewed by Pluot-Sigwalt et al. (2009) seems to be worldwide distributed associated to its prey.

Gynaikothrips ficorum Marchal (Thysanoptera: Thripidae) is a monophagous, gall-forming thrips of *Ficus microcarpa* L. f. (Moraceae) (Mound et al., 1996; Mound and Marullo, 1996; Tree and Walter, 2009). This species is commonly known as the Cuban laurel thrips (Paine, 1992) or thrips of *Ficus* trees. It has been distributed widely by the horticultural trade on the decorative *F. microcarpa* across all continents, except Antarctica (Mound, 2009).

The galls induced by these thrips reduce the photosynthetic activity of the plants and depreciate their ornamental value due to discolored and curled leaves. Further, adult thrips can be very annoying, landing and involuntarily biting people, causing skin irritation (Piu et al., 1992).

The gall formed by thrips represents a microcosm hosting all immature stages and thrips adults, their natural enemies, and other gall inquilines. Predatory species recorded upon *G. ficorum* include the thrips egg predator *Androthrips ramachandarai* (Karny) (Thysanoptera: Phlaeothripidae), heteropterans such as *M. confusa* Streito & Matocq, and the larvae of *Chrysoperla carnea* (Stevens) (Neuroptera: Chrysopidae) (Wolcott, 1953; Tawfik, 1967; Paine, 1992; Bennett, 1995; Held et al., 2005; Boyd and Held, 2006; Arthurs et al., 2011). Interestingly, like the adults of several other species among the Phlaeothripidae, both the pupae and the adults of *G. ficorum* exhibit a behavior that has been interpreted as egg defense against such intruders (Mound, 2004). The behavior – raising their abdomen toward the interloper while making quick backward and forward movements – is displayed both against other thrips walking in the gall and when nymphs and adults of *M. confusa* approach the eggs.

The first attempt to control *Gynaikothrips* with *M. confusa* (=*moraguesi*) was done in 1964 by introducing this predator from Manila, Filipinas, to the Pauoa Valley Island, Honolulu (Lewis, 1973). Further observations reported the establishment of the predator in this locale (Davis and Krauss, 1965). Over the ensuing decades, application of *M. confusa* has become an important way to control the Cuban laurel thrips, *G. ficorum*. In urban areas and especially on plants maintained indoors, its use is favored because of constraints upon the use of pesticides in such places. In addition, even on outdoor plants or in nurseries, where the use of insecticide sprays would be feasible, biological control with *M. confusa* offers better ability to reach the thrips inside the galls. Recently, Arthurs et al. (2011) released *M. confusa* into a greenhouse on *Ficus benjamina* L. plants infested with *Gynaikothrips uzeli* Zimmerman (Thysanoptera: Phlaeothripidae); five weeks later, they measured a 95% reduction in the thrips population and a 77% reduction in new gall formation.

The development of *G. ficorum* goes through eggs, two larval instars, two pupal stages and the adult stage (Mound and Kibby, 1998). Egg to adult development of *G. ficorum* at 25 °C lasts about 22 days and adult female produce, on average, 125 eggs (Paine, 1992; Mound and Marullo, 1996). Eggs are whitish with a sausage form and laid in groups on the leaf surface inside the gall. To gain a more complete understanding of the behavioral interactions between the predatory bug *Montandoniola* and its prey *Gynaikothrips*, the investigations reported here had three objectives: (i) to determine *M. confusa* predation rate on eggs, larvae/prepupae, and adults of *G. ficorum* when these were available in different densities, using the functional response to analyze the predatory behavior; (ii) to investigate the influence of adult (presumably parental) thrips in the gall on egg predation by *M. confusa*; and (iii) to determine the predation rate of *M. confusa* on eggs, larvae/prepupae, and adults of thrips when these were offered singly or simultaneously with other developmental stages in the gall across different ratios of these stages.

2. Materials and methods

Trials were carried out in the Biological Control Laboratory of the Universidade Federal Rural de Pernambuco (UFRPE), Recife, PE. Insects were collected in the field but later maintained in the laboratory, where they were reared and studied in growth chambers regulated to 12 h photophase and with temperature (25 ± 0.8 °C) and relative humidity (63 ± 8.8% R.H.) monitored at 30 min intervals.

2.1. Association of gynaikothrips and Montandoniola confusa

To accrue information about the distribution of the predator *M. confusa* in relation to thrips infestations throughout Brazilian territory, the authors and other collaborators conducted surveys on *Ficus* plants when galls were present on leaves. A minimum of 200 galls was inspected at each location, including several plants randomly chosen in the same place. The survey covered 11 Brazilian states and the Federal District, including all five Brazilian geographic regions. This procedure aimed only to verify whether the predator was also present where the thrips were damaging the plants; when present, the predator was collected to be identified. The thrips *G. ficorum* and *G. uzeli* are taxonomically closely related, as are the species of their host plants, *F. microcarpa* and *F. benjamina* including the cultivars. Thus, considering that *M. confusa* prey on *G. ficorum* and *G. uzeli* and can be present on both ficus species, the results of this survey are reported as prey on *Gynaikothrips* spp. and *Ficus* spp.

2.2. Predator and prey

The initial study populations of the predator *M. confusa* and its prey *G. ficorum* were gathered from galls collected on plants of *F. microcarpa* used in street landscape or plants used as green fencing in gardens. The plants were identified according to the exsicata No. 35333 deposited in the Herbarium "Prof. Vasconcelos Sobrinho" (UFRPE). Predator and prey were collected in Recife, PE and some neighboring cities (São Lourenço da Mata, Paudalho, Jaboatão dos Guararapes, and Camaragibe), but especially in Aldeia, County of Paudalho, PE (coordinates 7° 55′ 47.27″ S and 35° 02′ 28.45″ W).

In the laboratory the material was processed, transferring predator nymphs in the fourth and fifth instars to 80-mL transparent plastic containers (J. Prolab®, São José dos Pinhais, PR). Galls containing abundant eggs, larvae, pupae, and adults of thrips were provided as prey to the predator nymphs. Thrips were replaced every three days until predator nymphs molted to adult stage. Each day, adults of *M. confusa* were collected and segregated by sex. Adult sex can be determined by examining the last abdominal uromere, which is curved laterally on males (Pluot-Sigwalt et al., 2009). Later, male and female bugs were paired into plastic containers of 80-mL volume similar to those used to rear the nymphs.

Laboratory rearing provided additional *M. confusa* adults to multiply the colony and as a source of known-age adults for experimental trials. Adult anthocorids were offered thrips in all

developmental stages as prey. Galls containing eggs, nymphs, and adults were opened, and with the aid of a soft brush, thrips of different developmental stages were gently brushed into the predators' rearing containers. To provide moisture and an oviposition substrate, each container also included a section (~1 cm long) of green bean [*Phaseolus vulgaris* L. (Fabaceae)] that had been dipped into 5% sodium hypochlorite solution for 5 min, then washed with tap water, to reduce microorganism development.

The prey originated from field-collected galls or from galls produced by greenhouse-grown potted plants. Potted plants were kept indoors to guarantee prey availability during the rainy season, which in our location extends from April to September. This procedure was required due to the annual thrips population crash caused by the rainfall.

2.3. Functional response of Montandoniola confusa to different densities of Gynaikothrips ficorum

Adults of *M. confusa* 5–10 days old were used in this trial. To equalize their satiation levels, they were deprived of prey for 24 h prior to trial initiation, but they were provided with a section of green bean pod as a source of moisture during this period. Based on previous tests of predation rates (Tavares 2013), different numbers of prey were provided, depending upon the developmental stage of the thrips: 40, 60, 80, 100, 120, and 150 eggs; 1, 2, 8, 16 and 32 larvae/prepupae or adults. Treatments were established with eggs (13, 15, 15, 15, 8, and 9 replications), larvae/prepupae (15, 15, 15, 14, and 15 replications), and adults (17, 25, 22, 25, 28, and 24 replications). The different number of replications established was a result of logistics – the time and labor required to set up higher prey densities mandated a lower number of replications, variation in the results with adult thrips predation necessitated a greater number of replications, and only replications with live predators were considered in data analysis.

To study the predation capacity and preference of *M. confusa* upon different stages of *G. ficorum* in different densities, galls were collected in the field to assure a natural population structure in the microcosms. We used only young galls, characterized by folded leaves and the absence of chlorotic spots. We chose to include only galls that included pale, whitish eggs, indicating they were not close to eclosion. To obtain the respective prey densities we opened the galls to count the number of individuals present. We adopted the procedure of adding or taking out the superfluous prey items, except for the eggs which had densities adjusted only by taking the superfluous.

Galls containing eggs, larvae/prepupae, or adults in their respective densities were placed in glass vials of 2 cm diameter and 8 cm tall; immediately afterward, one predatory adult female anthocorid was released inside the vial containing the prey and the vial was closed with PVC film. To allow gas exchange and to avoid moisture formation inside the vial, small holes were punched into the PVC film using a number 0 insect pin. Simultaneously, three replications of each prey stage and density were set up without predators to measure prey natural mortality. Vials containing prey and predators were kept inside a climatic growth chamber regulated to 25 ± 1 °C, 65 ± 8% of relative humidity, and 12 h of photophase. The degree of predation upon thrips eggs, larvae/prepupae, and adults was recorded after 48 h. Eggs and larvae/prepupae attacked by the predator became shriveled in appearance; we considered adults to have been attacked when they were inactive.

The natural mortality in vials without a predator was less than 3.2% across all replications. Therefore, analyses were run without corrections for natural mortality. Based on the number of prey attacked (Na) as a function of the initial number of prey available (N0), the data on predation were analyzed using the two-step methodology of functional response. In the first step, the general shape of the functional response curve, which is based on a logistic regression of the number of prey consumed per density, was determined through the CATMOD procedure using SAS (SAS Institute, 1999). The cubic model was initially tested due to its capacity to detect the most possible functional response graph variations, and the sign of the linear coefficient of the equation obtained was used to determine the type of functional response, as described by Juliano (1993). The second step consisted of determining the handling time (T_h) and attack rate (a′) parameters of the functional response. These parameters were estimated with nonlinear least square regression based on the proportion of prey eaten (Na/N0) as a function of the initial prey densities (N0) (PROC NLIN; SAS Institute, 1999). The functional response parameters Th and a′ determined for *M. confusa* preying upon different stages of thrips were compared statistically using the 95% confidence interval mean overlapping procedure (Di Stefano, 2005).

2.4. Defense against predation

All developmental stages of *G. ficorum* can be found sharing the same gall. In these galls, it is common to observe thrips adults (presumed parents) standing over the eggs, displaying a defensive posture against conspecifics and predators. Thus, these trials compared egg predation by *M. confusa* with adult thrips present or absent in the gall.

To initiate the trials, we field-collected newly formed galls as described before. In the laboratory, these galls were inspected to remove other arthropods and to select those with recently laid egg batches and with adults present. Two treatments were set up. The first treatment consisted of galls with egg batches plus adult thrips (herein "+thrips"), and the second treatment consisted of galls with egg batches but without adult thrips (herein "−thrips"). A total of 67 galls hosting from 2 to 126 eggs and from 2 to 8 adult thrips per gall were exposed to egg predation by one *M. confusa* adult female per gall over a 24 h period. The second treatment consisted of 72 galls hosting from 11 to 117 eggs per gall; eggs in these galls were exposed to one female adult of *M. confusa* without adult thrips in the gall. Each gall was considered one replication. The variation on number of eggs per gall was maintained as collected from the field to avoid influencing the natural behavior of thrips. Predation exposure and evaluation procedures were similar to those for previous tests. After 24 h from releasing the predator, each gall was opened under a stereomicroscope (10–40x) to record the number of eggs that had been preyed upon. In the treatment +thrips, the number of unpreyed eggs was also determined to adjust the number of eggs available initially, considering that the female kept in the gall might lay more eggs during the 24 h observation period. The number of adult thrips killed was also recorded. These data (not shown) indicate a range of 0–2 dead adult thrips per gall irrespective of egg density or number of adult thrips initially present.

The hypothesis of adult thrips interference on predation of eggs by *M. confusa* was analyzed by using Proc ANOVA of SAS (SAS Institute, 1999) to compare the treatments +thrips and −thrips in the gall as function of egg densities per gall and the interaction of egg densities and treatments. Moreover, the number of preyed-upon eggs as a function of the initial egg density in the gall was calculated using the regression analysis performed by Proc REG of SAS selecting the equation with significant parameters ($P < 0.05$) and the greatest coefficient of determination (R). Furthermore, to test the hypothesis that thrips adult presence in the gall might change egg predation across the densities of eggs in the galls, the linear fitted models were compared. Thus, the linear slopes of fitted models of egg predation as function of egg densities in the galls were compared between treatments +thrips and −thrips using PROC MIXED of SAS to test the equality of linear slopes (SAS Institute, 1999).

2.5. Predation preference upon thrips stages

This trial was set up to investigate prey consumption by *M. confusa* when all thrips developmental stages were simultaneously present in the gall compared to consumption when only a single stage was available. According to Cock (1978), preference behavior exhibited by a predator is only accurately assessed when the result is maintained under the condition of variable prey availability. Thus, the trial was conducted with varying proportions of the prey stages.

As before, galls containing recently laid eggs were selected from field collections. In the laboratory, we adjusted the egg densities by taking out the superfluous eggs in the gall, then adding or removing larvae/prepupae and adults to compose the treatments assigned to the proportions of these prey items. For these prey preference trials, larvae and adults added came from different galls to avoid the potential of parental behavior protecting the eggs. Treatments consisted of prey availability in different proportions in a manner that corresponded to either prey abundance or prey scarcity for each prey stage, whether provided alone or with other prey stages. Thus, the treatments included these ratios, respectively, of eggs:larvae/prepupae:adults – 05:25:25 (12 replications); 10:20:20 (12 replications); 20:15:15 (15 replications; 30:10:10 (12 replications); and 50:05:05 (13 replications). Treatments consisting of only a single available prey stage included 80 eggs (20 replications); 20 larvae/prepupae (15 replications); and 20 adults (14 replications).

The procedure adopted to expose prey to predation by *M. confusa* was similar to that for the previous trials. After 24 h of prey exposure to one *M. confusa* adult female the number of prey items killed was recorded. Furthermore, to allow comparisons of predation within and among treatments, the number of prey of each stage that had been killed was transformed into percentage of prey consumed as function of the initial prey density. Then, the data were tested under the null hypothesis that no prey preference implies the expectation of an equal percentage of predation regardless of prey proportion. These analyses were performed using the Proc Freq of SAS (SAS Institute, 1999), and interpretation was drawn through chi-square testing at 5% significance level.

3. Results

3.1. Association of Gynaikothrips and Montandoniola confusa

From collections made in 36 locales covering five geographic regions of Brazil (Fig. 1), *Gynaikothrips* spp. were present in all places where the plants of *Ficus* spp. were also present. Among all sites surveyed (36), *M. confusa* was not found at nine specific sites (25%) but this predator was present in other locations in the same region (Fig. 1).

Region	Locale- State	Thrips	Predator
Northeast	Recife - PE	+	+
	Surubim - PE	+	+
	Petrolina - PE	+	+
	Paudalho - PE	+	+
	Juazeiro - BA	+	+
	Arrail d'Ajuda - BA	+	-
	Eunápolis - BA	+	+
	Teotonio Vilela - AL	+	+
	Propriá - SE	+	+
	João Pessoa - PB	+	+
	Natal - RN	+	+
Midwest	Nova Mutum - MT	+	-
	Rio Verde - GO	+	-
	Brasília - DF	+	+
	Dourados - MS	+	-
	Rondonópolis - MT	+	+
Southeast	Vitória - ES	+	+
	Pedro Canário - ES	+	+
	Jaboticabal - SP	+	+
	Alegre - ES	+	-
	Juiz de Fora - MG	+	+
	Viçosa - MG	+	+
North	Boa Vista- RR	+	-
	Japurá - AM	+	+
	Iranduba - AM	+	+
	Rio Preto da Eva-AM	+	+
	Manaus - AM	+	+
	Marabá - PA	+	+
South	Joivile - SC	+	-
	Araucária - PR	+	+
	Arapoti - PR	+	+
	Londrina - PR	+	-
	Tomazina - PR	+	+
	Venceslau Bráz - PR	+	+
	Porto Alegre - RS	+	-
	Curitiba - PR	+	+

Fig. 1. Occurrence of gall-forming thrips *Gynaikothrips* spp. and of its predator *Montandoniola confusa* from surveys in different locales of Brazil.

Four species of coccinellids were also collected and identified during the collections made in the State of Pernambuco: *Chilocorus nigrita* (Fabr.), *Harpasus quadrifolium* Gonzales Corrêa & Almeida, *H. paladabris* and *Delphastus* sp. These predatory ladybird beetles were found associated with galls of *F. microcarpa* infested with the whitefly *Singhiella simplex* (Singh) (Hem.: Aleyrodidae).

3.2. Functional response of Montandoniola confusa to different densities of Gynaikothrips ficorum

The predation rate of female *M. confusa* upon *G. ficorum* varied as a function of the tested developmental stage of the thrips (i.e., eggs, larvae/prepupae, and adults) and the initial density of the prey (N0) available to the predator (Table 1 and Fig. 2). The average rate of egg predation was significantly higher compared to predation upon larvae/prepupae and adults; however, predation rates on these last two stages were statistically similar (Table 2).

The effect of prey density revealed a type II functional response for *M. confusa* females preying upon all tested stages of *G. ficorum* (Table 1). This outcome agrees with the decreasing proportion of prey attacked as function of prey availability (Fig. 2 – graphics at right). The predation behavior, characterized by a type II functional response, indicates that the searching rate is linear as a function of initial prey availability ($a' = bN$). Further, the searching rate was limited by the area available to the predator, consisting of galls of nearly the same size across all tested densities. Therefore, the number of prey attacked could be calculated by the ratio between the exposure time to predation (48 h) and the handling time per prey item attacked (T_h). This result showed that the predation by *M. confusa* upon thrips eggs was significantly higher across the

Table 1
Estimated parameters of the logistic regression between the proportion of eggs, larvae/prepupae, and adults of *Gynaikothrips ficorum* attacked by *Montandoniola confusa* at initial prey densities between 40 and 150 eggs and between 2 and 32 larvae/prepupae or adult thrips per *Ficus microcarpa* gall.

Thrips	Parameters	Values (±SE)	DF	χ^2	*P*
Eggs	Intercept	3.3534 ± 0.2100	1	125.72	<0.0001
	Linear	−0.0309 ± 0.0059	1	26.64	<0.0001
	Quadratic	$9.5 \times 10^{-5} \pm 2.8 \times 10^{-5}$	1	11.36	0.0008
Larvae/prepupae	Intercept	2.2653 ± 0.3354	1	47.61	<0.0001
	Linear	−0.1668 ± 0.0398	1	17.55	<0.0001
	Quadratic	$0.0023 \pm 9.6 \times 10^{-4}$	–	6.00	0.0143
Adults	Intercept	1.4911 ± 0.1254	1	141.48	<0.0001
	Linear	−0.0620 ± 0.0050	1	149.19	<0.0001
	Quadratic	–	–	–	–

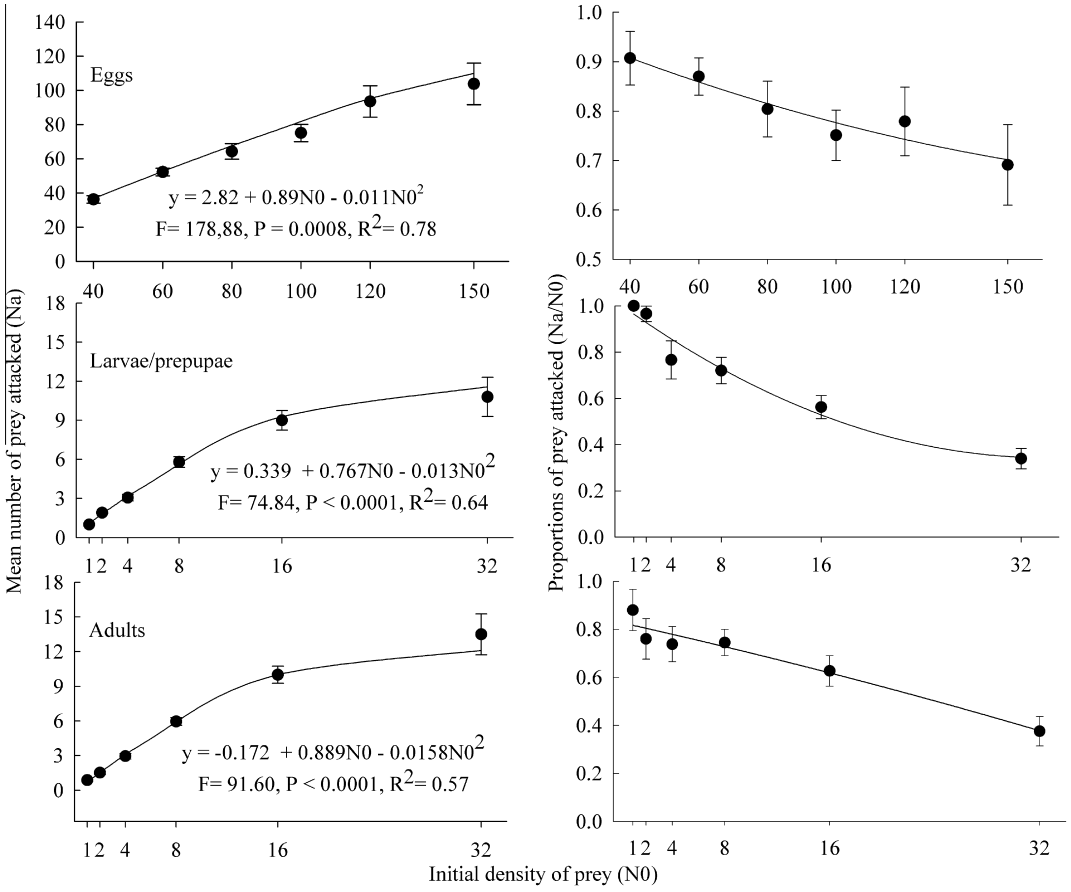


Fig. 2. Left: Average number of eggs, larvae-prepupae and adults of *Gynaikothrips ficorum* preyed (Na) and; right: proportions of eggs, larvae-prepupae and adults preyed (Na/N0) by adults of *Montandoniola confusa* as function of the initial prey densities (N0) during 48 h of exposure to predation in galls of *Ficus microcarpa*.

Table 2
Mean values (95% confidence intervals) of searching rate [a′ (h^{-1})] and handling time [T_h (h)] for *Montandoniola confusa* feeding on eggs, larvae/prepupae or adults of *Gynaikothrips ficorum* in galls of *Ficus microcarpa* and estimated number of prey attacked during the observation period (T = 48 h/Th).

Thrips stages[a]	Searching rate – a′	Handling time – T_h	T/T_h
Eggs	0.00108 b (0.0005–0.0016)	0.41 b (0.32–0.48)	117.0 a (100.0–150.0)
Larvae/prepupae	0.008 a (0.003–0.015)	4.44 a (3.87–5.01)	10.8 b (9.58–12.4)
Adults	0.007 a (0.003–0.012)	3.88 a (3.39–4.38)	12.3 b (10.9–14.1)

[a] Means followed by the same letter in the column are not significantly different, 95% confidence intervals overlapping rule.

tested densities compared to predation upon larvae/prepupae and adult thrips (Table 2).

3.3. Adult defense against predation

The number of *G. ficorum* eggs preyed upon by *M. confusa* varied as a function of egg density per gall (F_{df} = 3, 131 = 94.05, P < 0.0001), as a function of the treatments +thrips and −thrips in the galls (F_{df} = 1, 131 = 93.75, P < 0.0001), and as a function of the interaction of the treatments and egg densities (F_{df} = 3, 131 = 8.44, P < 0.0001). Egg predation by *M. confusa* increased linearly in both treatment conditions (−thrips: $y = 6.96 + 0.779x$, F = 556.16, P < 0.0001, r^2 = 0.88; +thrips: $y = 9.72 + 0.449x$, F = 52.58, P < 0.0001, r^2 = 0.44). Furthermore, egg predation as a function of egg densities was statistically higher in the treatment in which adult thrips were absent from the galls (−thrips) (Proc Mixed of SAS for equality of linear coefficient: $\beta_1 - \beta_2 = 0.27 \pm 0.06$, t_1, 134 = 4.00, P = 0.0001) (Fig. 3A).

The influence of adult thrips in the gall on protecting eggs from predation by *M. iconfusa* was statistically significant only on densities of over 30 eggs per gall, a result that explains the interaction of egg densities and treatments +thrips and −thrips on egg predation (Fig. 3B). At lower egg densities (<30 eggs per gall), egg loss was not affected by the presence of adult thrips in the gall (P = 0.3866). The difference on number of eggs preyed upon between the treatment +thrips and −thrips varied from 4.2% for egg densities below 30 eggs per gall to ~50% for egg densities of over 90 eggs per gall (average of eggs preyed ± SE, +thrips, 42.0 ± 16.26; and −thrips, 84.8 ± 5.47 eggs). Egg predation rates became more variable as egg densities per gall increased (greater error bars in Fig. 3B for egg densities >31 eggs per gall). As a result, although egg predation decreased numerically as the number of adult thrips in the gall increased (1–8), the change was not large enough to show a statistically significant difference (y = 99.39–2.51x, r^2 = 0.09, P = 0.68).

3.4. Predation preference upon thrips stages

Simultaneous exposure of the predator to different proportions of thrips in all stages of development indicates that *M. confusa* clearly prefers thrips eggs over larvae/prepupae and adults (Table 3). Despite varying the proportional availability of number of eggs and subsequent developmental prey stages, egg consumption was always higher (85–100%, Table 3). Furthermore, irrespective of varying the absolute number of different prey stages in the galls, the predation of eggs was always equally high, whereas predation upon larvae/prepupae and adults lessened with increasing availability of eggs.

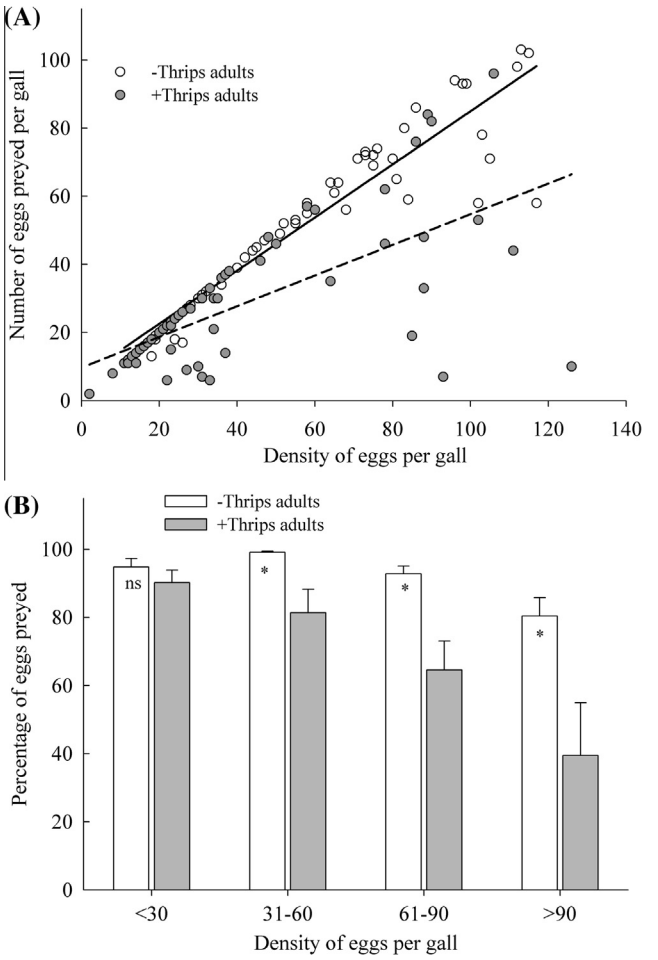


Fig. 3. Predation of *Gynaikothrips ficorum* eggs by *Montandoniolla confusa* under the condition of presence (+thrips) and absence (−thrips) of the thrips adult in the gall. A: Number of eggs preyed as function of egg densities in the gall; and B: Mean percentage of egg preyed considering four class of number of eggs per gall. *Asterisks stand for significant difference between the treatments +thrips and −thrips (Fisher's test from ANOVA), and ^{ns} stands for no significant difference at 0.05 significance level.

4. Discussion

The "snap-shot" survey adopted in this study aimed only to show the association of the predator and its thrips prey, and results showed clearly that the predator *M. confusa* and the gall-forming thrips *G. ficorum* are associated and spreading alongside one another throughout Brazil. This is the first report of *M. confusa* in South America. Because both thrips and predator occur together in the gall, it is likely that they are being spread through ornamental plant marketing.

In all locales where the predator was found, different developmental stages of the predator were present in the gall. Predator eggs are inserted into the gall tissue around or in the middle of the thrips eggs, while nymphs run freely inside the gall. Moreover, adult predators can leave the gall when the galls are opened, but quickly enter another nearby gall. Thus, a straight association of the predator with its prey is established in the microcosm that is formed by the gall induced by the thrips in the field. This supports

Table 3
Predation upon eggs (E), larvae/prepupae (LP) and adults (A) of *Gynaikothrips ficorum* by *Montandoniola confusa* under different proportions of prey stages available in the gall of *Ficus microcarpa*.

E - LP – A (replications)	Percentage of prey consumed (Average of prey consumed)			[a]χ^2-test$^{P\text{-value}}$
	Eggs	Larvae/prepupae	Adults	
05-5-25 (12)	100 ± 0 A (5.0)	35.6 ± 5.07 Ba (8.7 ± 1.15)	13.6 ± 4.01Cb (3.7 ± 0.93)	df = 2, $\chi^2 = 39.81^{<0.0001}$ df = 1, $\chi^2 = 4.22^{0.0395}$
10-20-20 (12)	100.0 ± 0 A (10.0)	50.4 ± 3.19 Ba (10.1 ± 0.60)	47.7 ± 7.03 Ba (10.0 ± 1.41)	df = 2, $\chi^2 = 13.67^{0.0013}$ df = 1, $\chi^2 = 10.20^{0.6506}$
20-15-15 (15)	100.0 ± 0 A (20.0)	43.8 ± 4.06 Ba (6.6 ± 0.61)	50.0 ± 7.27Ba (7.5 ± 1.09)	df = 2, $\chi^2 = 13.46^{0.0012}$ df = 1, $\chi^2 = 0.205^{0.6852}$
30-10-10 (12)	99.4 ± 1.92 A (29.6 ± 0.01)	40.8 ± 5.95 Ba (4.1 ± 0.59)	21.6 ± 8.15Ba (2.4 ± 0.54)	df = 2, $\chi^2 = 29.13^{0.0001}$ df = 1, $\chi^2 = 2.44^{0.1178}$
50-05-05 (13)	85.2 ± 5.96 A (42.7 ± 3.47)	21.5 ± 6.02 Ba (0.7 ± 0.31)	13.5 ± 3.18 Ba (0.3 ± 0.19)	df = 2, $\chi^2 = 35.66^{<0.0001}$ df = 1, $\chi^2 = 1.07^{0.3008}$
80-00-00 (20)	78.9 ± 4.72 (62.4 ± 4.25)	–[b]	–	–
00-20-00 (15)	–	25.5 ± 4.10 (5.2 ± 0.82)	–	–
00-00-20 (14)	–	–	22.5 ± 3.50 (4.2 ± 0.67)	–

[a] df (degree of freedom = 2) stands for chi-square results testing the hypotheses for equal percentage of predation across all thrips stages (E, LP, and A) represented by capital letters; df = 1 stands for chi-square results testing the hypotheses for equal percentage of predation between LP and A represented by small letters.
[b] No values due to the treatment design.

the previously observed correlation of population dynamics between *M. confusa* and the prey *G. ficorum* (Paine, 1992).

The close association of *M. confusa* with its prey is an important asset for any consideration of this species' potential use in biological control. The presence of all stages of both the predator and the prey within a spatially limited microcosm creates a situation similar to that encountered in other studies that have focused on mosquito larvae and their predators in such varied situations as treeholes (Edgerly et al., 1999; Griswold and Lounibos, 2006), pitcher plants (Miller and terHorst, 2012), and bromeliads (Richardson, 1999). The issue of spatial limitation has meaning for predator–prey interactions because the relative areas available for prey escape and for predator searching constitute one of the most important sets of variables affecting predation rates in the field (Wiedenmann and O'Neil, 1992. This has the potential to create a discrepancy between field and laboratory results (Oliveria et al., 2001), but in our study, the laboratory set-up closely mimicked that which would occur in the field, and thus our results could easily be extrapolated.

Another major obstacle that can hinder the widespread use of a predaceous insect species in applied biological control is predator dispersion from releasing sites (Neves et al., 2009). Predators are generalists with few exceptions, and by being generalists they prefer sites where guarantee prey availability. In many cases, the places with abundant prey and sites most favorable to the predator might not be the crop field hosting the pest species targeted by the release.

As estimated through the handling time (T_h) of the functional response and total time of observation (T/T_h), predation rates for eggs, larvae/prepupae and adults of thrips and their respective confidence intervals show strong model prediction based on the observed data (Table 2 and Fig. 2 left). For instance, the mean prey consumption in the highest prey densities available was 103.7 eggs, 10.8 larvae/prepupae, and 12.3 adults, respectively (Fig. 2). These results characterize the power of the functional response parameters calculated to reproduce the estimation of the predation of different thrips stages available in the gall.

As our results demonstrate, *M. confusa* prey upon all developmental stages of thrips when they are singly available. This finding agrees with a report published under the older name *Macrotrachiella nigra* Parshley (=*M. confusa* after Pluot-Sigwalt et al., 2009) in which this predator consumed, on average, 12.6 adults and 8.5 larvae of *G. ficorum* when having available 75 adults or 75 larvae, respectively (Paine, 1992). However, their predation has a greater impact on eggs than on larval and adult stages. Corroborating this, searching rate and handling time were significantly lower for predators preying upon eggs (Table 2). The preference of *M. confusa* for consuming thrips eggs has also been noted with the conspecific thrips species *G. uzeli* (Arthurs et al. (2011).

Defensive behavior by adult thrips did not change this preference (Fig. 3 and Table 3). The presence of adult thrips resulted in lower egg predation only under conditions of high egg availability, when the predator is likely already satiated and prey availability is, on average, higher than the number of eggs consumed per day (≈80 eggs, Table 3).

Why does *M. confusa* prefer thrips eggs? On one level, the greater predation on thrips eggs might be explained by superior nutritional quality of the eggs as food, and the fact that under most conditions they are more abundantly available compared to subsequent developmental stages. Predatory heteropterans such as anthocorids and geocorids which feed on different developmental stages of their prey usually achieve superior performance preying upon eggs (Torres et al., 2004; Jalalizand et al., 2011). On another level of explanation, these eggs presumably do not offer resistance against predatory attack; they can neither fight nor flee, whereas larval, pupal, and adult stages of *G. ficorum* might exhibit anti-predator behavior that reduces predatory success and biological performance.

Across the animal kingdom, relative prey shortage or abundance affects behavior in powerful ways. For *Montandoniola* (and perhaps a wide range of other predatory heteropterans) encountering adequate numbers of gall inhabitants of all ages and/or potential satiation, the balance of benefits (nutritional quality, ease of capture) versus costs (potential interference from guarding adults, anti-predator defenses of larvae and adults) might be expected to swing in the direction of egg predation. Predation on advanced developmental stages of *Thrips tabaci* Lindman (Thysanoptera: Thripidae), for example, was also reduced when the predatory mites *Neoseiulus barkeri* Hughes and *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) became satiated (Bakker and Sabelis, 1989). Under intermediate conditions of progressively lower prey availability, the predator might be expected to become increasingly prone to disregard the attentions of defensive thrips adults and to attack other thrips life stages.

A predator's attack and subsequent successful ingestion and conversion of that prey into new predators are key processes that indicate the biological performance of the predator and its potential to regulate a pest population (Hassell, 1978; Torres et al., 2004; Brito et al., 2009). Our data indicate that when 5–30 eggs per gall day^{-1} are available to them, adult *M. confusa* generally prey upon 100% of the eggs in the gall plus additional larvae and adults of thrips if available (Fig. 3 and Table 3). Egg densities <30 eggs suggest prey shortage and stimulate greater predation on thrips larvae and adults, but increasing egg availability, a situation that is common in the galls found in the field, will sustain the predator that avoids preying upon larvae and adults. As others have noted (Cock, 1978; Chesson, 1983; Butler et al., 2008; Xu and Enkegaard, 2010), changes in predator prey preference might be predicted to occur

when prey availability is variable and, therefore, the use of a range of prey combinations is a recommended methodology to test prey preference. It is interesting to note that despite preferring to prey upon eggs, *M. confusa* feeds upon and develops using all thrips stages, a flexible strategy that allows the predator to sustain its population in the field irrespective of the prey stage available. It is possible that in some situations they may even feed upon non-related arthropods; although they are essentially thrips feeders, anthocorid predators have also been reported feeding upon lepidopteran eggs, whiteflies, mites, and aphids (Lattin, 2000; Xu and Enkegaard, 2009; van Lenteren, 2011).

Even when records are included for *M. moraguesi* and *M. nigra*, now considered synonymous with *M. confusa* (Pluot-Sigwalt et al., 2009), there are few published studies on the biology and predation behavior of this predator group. However, there have been two recent investigations with *Montandoniola*. Arthurs et al. (2011) conducted an excellent study of *M. confusa* from prey preference to greenhouse release, showing its potential to control the thrips species, *G. uzeli*. Yamada et al. (2011) published the description and biology of a related species, *Montandoniola indica* Yamada, that preys upon the pepper gall-forming thrips, *Liothrips karnyi* Bagnall (Thysanoptera: Phlaeothripidae). In their trials in Petri dishes, these latter authors report that *M. indica* in the first and second instar preferred to prey upon eggs of thrips, while older nymphal stages and adults of the predator preferred to prey upon adult thrips. During 24 h-observation periods, females and males of *M. indica* killed an average of 4.2 and 2.8 adults of *L. karnyi*, respectively. Yet, the ingestion time observed for five adult females varied from 12 to 74 min for first and second prey attacked and several hours for subsequent thrips attacked (time not specified). Moreover, it is known that the first prey item attacked by predatory heteropterans is handled more quickly than subsequent prey items due to the satiation level of the predator (Cohen, 1998). Also, the average number of thrips attacked by *M. confusa* during the observation period in our study was about 3-fold the average number of thrips attacked by *M. indica* (i.e., 12.3 versus 4.2 thrips). In fact, it is important to highlight that the anthocorid genus *Montandoniola* seems to offer an entire group of potentially useful predators to expand our ability to target different species of gall-forming thrips.

Acknowledgments

We are grateful to several people that helped us to check for thrips and predator associations in various locales in Brazil: Cristina S. Bastos-UnB, José Adriano Giori-UFPA, Elisângela Morais-Embrapa Roraima, Cácia Tigre-UFGD, and Alessandra Marieli Vaccari-UNESP Jaboticabal. The remaining locations were surveyed by A.M.T and J.B.T. Also we are in debt to Prof. José Adriano Giorgi – UFPA for identifying the Coccinellidae species and to Dr. Diego Leonardo Carpintero (División Entomologia, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia") for identifying our predator.

References

Arthurs, S., Chen, J., Dogramaci, M., Ali, A.D., Mannion, C., 2011. Evaluation of *Montandoniola confusa* Streito and Matocq sp. nov. and *Orius insidiosus* Say (Heteroptera, Anthocoridae), for control of *Gynaikothrips uzeli* Zimmerman (Thysanoptera, Phlaeothripidae) on *Ficus benjamina*. Biol. Control 57, 202–207.

Bakker, F.M., Sabelis, M.W., 1989. How larvae of *Thrips tabaci* reduce the attack success of phytoseiid predators. Entomol. Exp. Appl. 50, 47–51.

Bennett, F.D., 1995. *Montandoniola moraguesi* (Hemiptera, Anthocoridae), a new immigrant to Florida, friend or foe? Vedalia 2, 3–6.

Boyd Jr., D., Held, D.W., 2006. *Androthrips ramachandrai* (Thysanoptera, Phlaeothripidae), an introduced thrips in the United States. Fla. Entomol. 89, 455–458.

Brito, E.P.J., Gondim Jr., M.G.C., Torres, J.B., Fiaboe, K.K.M., Moraes, G., Knapp, M., 2009. Predation and reproductive output of the ladybird beetle *Stethorus tridens* preying on tomato red spider mite *Tetranychus evansi*. Biocontrol 54, 363–368.

Butler, C.D., ÓNeil, R.J., 2008. Voracity and prey preference of insidious flower bug (Hemiptera, Anthocoridae) for immature stages of soybean aphid (Hemiptera, Aphididae) and soybean thrips (Thysanoptera, Thripidae). Environ. Entomol. 37, 964–972.

Chesson, J., 1983. Estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Cock, M.J.W., 1978. The assessment of preference. J. Anim. Ecol. 47, 805–816.

Cohen, A.C., 1998. Solid–to–liquid feeding, the insect(s) story of extra–oral digestion in predaceous Arthropoda. Am. Entomol. 44, 103–116.

Davis, C.L., Krauss, N.L.H., 1965. Recent introductions for biological control in Hawaii. X. Proc. Hawaiian Entomol. Soc. 19, 87–90.

Di Stefano, J., 2005. Effect size estimates and confidence intervals, an alternative focus for the presentation and interpretation of ecological data. In: Burk, A.R. (Ed.), New Trends in Ecology Research. Nova Science, New York, pp. 71–102.

Dobbs, T.T., Boyd, D.W., 2006. Status and distribution of *Montandoniola moraguesi* (Hemiptera, Anthocoridae) in the continental United States. Fla. Entomol. 89, 41–46.

Edgerly, J.S., Willey, M.S., Livdahl, T., 1999. Intraguild predation among larval treehole mosquitoes, *Aedes albopictus*, *Ae. aegypti*, and *Ae. triseriatus* (Diptera, Culicidae), in laboratory microcosms. J. Med. Entomol. 36, 394–399.

Griswold, M.W., Lounibos, L.P., 2006. Predator identity and additive effects in a treehole community. Ecology 87, 987–995.

Hassell, M.P., 1978. The dynamics of arthropod predator–prey systems. Princeton, Princeton University Press, p. 237.

Held, D.W., Boyd, D., Lockley, T., Edwards, G.B., 2005. *Gynaikothrips uzeli* (Thysanoptera, Phlaeothripidae) in the Southeastern United States, distribution and review of biology. Fla. Entomol. 88, 538–540.

Jalalizand, A., Modaresi, M., Tabeidian, S.A., Karimy, A., 2011. Functional response of *Orius niger niger* (Hemiptera, Anthocoridae) to *Tetranychus urticae* (Acari, Tetranychidae), effect of host plant morphological feature. IPCBEE 9, 92–96.

Juliano, S.A., 1993. Nonlinear curve fitting, predation and functional response curves. In: Scheiner, S.M., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Chapman and Hall, New York, pp. 159–182.

Lattin, J.D., 2000. Importance of minute pirate bugs (Anthocoridae). In: Schaefer, C.W., Panizzi, A.R. (Eds.), Heteroptera of Economic Importance. CRC Press, Boca Raton, pp. 607–637.

Lewis, T., 1973. Thrips, Their Biology, Ecology and Economic Importance. Academic Press, London.

Miller, T.E., terHorst, C.P., 2012. Testing successional hypotheses of stability, heterogeneity, and diversity in pitcher-plant inquiline communities. Oecologia 170, 243–251.

Mound, L.A., 2004. Australian Thysanoptera – biological diversity and a diversity of studies. Aust. J. Entomol. 43, 248–257.

Mound, L.A., 2009. Thysanoptera (Thrips) of the world – a checklist. Disponível em, <http.//www.ento.csiro.au/thysanoptera/worldthrips.html>. Accessed 07.01.2012.

Mound, L.A., Kibby, G., 1998. Thysanoptera, An identification guide, 2nd ed. CAB Internat, New York.

Mound, L.A., Marullo, R., 1996. The Thrips of Central and South America, An Introduction (Insecta, Thysanoptera). Memoirs on Entomology International. Associated Publishers, Gainesville, Florida.

Mound, L.A., Crespi, B.J., Kranz, B., 1996. Gall-inducing Thysanoptera (Phlaeothripidae) on *Acacia* phyllodes in Australia, host-plant relations and keys to genera and species. Invert. Taxonomy 10, 1171–1198.

Neves, R.C., Torres, J.B., Vivan, L.M., 2009. Reproduction and dispersal of wing-clipped predatory stinkbugs, *Podisus nigrispinus* in cotton fields. Biocontrol 54, 9–17.

Oliveria, J.E.M., Torres, J.B., Carrano-Moreira, A.F., Zanuncio, J.C., 2001. Efeito da densidade da presa e do acasalamento na taxa de predação de fêmeas de *Podisus nigrispinus* (Dallas) (Heteroptera, Pentatomidae) em condições de laboratório e campo. Neotrop. Entomol. 30, 647–654.

Paine, T., 1992. Cuban laurel thrips (Thysanoptera, Phlaeothripidae) biology in Southern California, seasonal abundance, temperature dependent development, leaf suitability, and predation. Ann. Entomol. Soc. Am. 85, 164–172.

Piu, G., Ceccio, S., Garau, M.G., Melis, S., Palomba, A., Pautasso, M., Pittau, F., Ballero, M., 1992. Itchy dermatitis from *Gynaikothrips ficorum* March in a family group. Allergy 47, 441–442.

Pluot-Sigwalt, D., Streito, J.C., Matocq, A., 2009. Is *Montandoniola moraguesi* (Puton, 1896) a mixture of different species? (Hemiptera, Heteroptera, Anthocoridae). Zootaxa 2208, 25–43.

Richardson, B.A., 1999. The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. Biotropica 31, 321–336.

SAS Institute, 1999. SAS/STAT user's guide, version 8.02, TS level 2 MO. SAS Institute Inc., Cary, NC.

Tawfik, M.F.S., 1967. Microfauna of the leaf-rolls of *Ficus nitida* Thunb. Hort. Bull. Soc. Entomol. Egypt 51, 483–487.

Torres, J.B., Silva-Torres, C.S.A., Ruberson, J.R., 2004. Effect of two prey types on life-history characteristics and predation rate of *Geocoris floridanus* (Heteroptera, Geocoridae). Environ. Entomol. 33, 964–974.

Tree, D.J., Walter, G.H., 2009. Diversity of host plant relationships and leaf galling behaviours within a small genus of thrips – *Gynaikothrips* and *Ficus* in southeast Queensland, Australia. Aust. J. Entomol. 48, 269–275.

van Lenteren, J.C., 2011. The state of commercial augmentative biological control, plenty of natural enemies, but a frustrating lack of uptake. Biocontrol 57, 1–20.
Wiedenmann, R.N., O'Neil, R.J., 1992. Searching strategy of the predator *Podisus maculiventris* (Say) (Heteroptera, Pentatomidae). Environ. Entomol. 21, 1–9.
Wolcott, G.N., 1953. Control of the Cuban laurel thrips *Gynaikothrips ficorum*. J. Agric. Univ. Puerto Rico 37, 234–240.
Xu, X., Enkegaard, A., 2009. Prey preference of *Orius sauteri* between Western flower thrips and spider mites. Entomol. Exp. Appl. 132, 93–98.
Xu, X., Enkegaard, A., 2010. Prey preference of the predatory mite, *Amblyseius swirskii* between first instar Western flower thrips *Frankliniella occidentalis* and nymphs of the two-spotted spider mite *Tetranychus urticae*. J. Insect Sci. 10, 1–11.
Yamada, K., Bindu, K., Nasreem, A., Nasser, M., 2011. A new flower bug of the genus *Montandoniola* (Hemiptera, Heteroptera, Anthocoridae), a predator of gall-forming thrips on black pepper in southern India. Acta Entomol. Musei Nat. Pragae 51, 1–10.